How did they get here from there? Detecting changes of direction in terrestrial ranging

Article (Accepted Version)

How did they get here from there?
Detecting changes of direction in terrestrial ranging.

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[*Animal Behaviour*, in press.]

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Abstract

Efficient exploitation of large-scale space is crucial to many species of animal, but the difficulties of studying how animals decide on travel routes in natural environments have hampered scientific understanding of environmental cognition. Field experiments allow researchers to define travel goals for their subjects, but practical difficulties restrict large-scale studies. In contrast, data on natural travel patterns are abundant and easy to record, but hard to interpret without circularity and subjectivity when making inferences about when and why an animal began heading to a particular location. We present a method of determining objectively the point at which an animal's travel path becomes directed at a location, for instance a distant feeding site, based on the statistical characteristics of its route. We evaluate this method and illustrate how it can be tailored to particular problems, using data that is (a) synthetic; (b) from baboons, where travel is from a single sleeping site in an overlapping home range, and (c) from chimpanzees, where sleeping sites are unlimited within a large territory. We suggest that this 'change-point test' might usefully become a routine first step in interpreting the decision-making behind animal travel under natural conditions.

Key words: baboon, change-point, chimpanzee, direction, route choice, cognitive map, statistical method.

Knowledge of home range is a potent survival weapon for an animal, reducing uncertainty about the location and availability of resources and sometimes allowing anticipation of danger. However, if the array of resources and dangers is large and varies with time, and the animal's home range is extensive, memory may present a significant challenge, potentially driving an evolutionary increase in brain size. Thus, the relatively large brains of simian primates have been argued to reflect selection for efficiency in storing and using knowledge about resources distributed through an extensive home range (Clutton-Brock and Harvey 1980; Mackinnon 1978; Milton 1981, 1988). In birds, hippocampal enlargement is associated with the habit of food storing, and this has been explained by suggesting that a larger hippocampus allows a bird to re-find more food caches (see Clayton and Lee 1998 for review). Testing these theories, however, has been severely limited by practical difficulties.

Animal knowledge of spatial areas that can be viewed from a single point has been studied extensively. Experiments have been used to investigate memory for what, where and when food has been stored, and who among the potential competitors might have observed them caching the food (Bugnyar 2002; Bugnyar and Heinrich 2005; Clayton et al. 2001; Dally et al. 2006; Emery and Clayton 2001; Shettleworth 1998). In contrast, rather few studies have investigated memory for large-scale space. The problem for field researchers is that they cannot generally know what prior plan (if any) is in the mind of the subject whose ranging behaviour they record. A few pioneering studies have circumvented this issue by using field experiments. Capitalizing on certain species' readiness to accept artificial food, researchers have investigated the response to variations of spatial pattern and temporal availability (e.g. in bees, Dyer 1991, Dyer, Berry and Richard 1993, Menzel et al 1999; in capuchin monkeys, Janson 1998, 2007). Capitalizing on the human-taught 'language' abilities of a captive chimpanzee that had access to a substantial outdoor enclosure, Menzel (1999) was able to give the chimpanzee instruction about the location of food and examine the strategy it employed to reach it.

Under natural conditions, however, interpretation of actual travel routes is potentially ambiguous. Consider for illustration the case of a frugivorous animal foraging in a closed woodland environment: perhaps an ape, a curassow, or a peccary. The path of a focal individual can be more-or-less exactly mapped, e.g. using GPS samples at regular intervals that are short compared to the animal's frequency of changing direction. At the same time, the place and time of resource acquisition can be recorded, and the amount consumed can be estimated. From these data, it may be possible to deduce something of the cognitive abilities needed to explain the behaviour (e.g. see Cunningham and Janson 2007; di Fiore and Suarez 2007; Garber 1988; Garber 1989; Janson and van Schaik 1988; Noser and Byrne 2007a, b). But such deduction is always indirect, and reliant on often unverifiable assumptions about the animal's own goals. Suppose a focal animal travelled in a generally SW direction during the day, on a somewhat zigzag path, finally arriving at a very large fruit resource. Did it move from tree to tree guided by sight or smell over the relatively small distances involved, and was merely lucky to arrive eventually at a greater-than-average resource? Or did it plan all along to reach the bumper harvest, and were all its travel decisions ultimately devoted to this single purpose? A researcher, examining the animal's mapped route afterwards, may be convinced that elaborate planning was involved: but how can such intuitions be quantified, avoiding circular reasoning and subjective judgements? It is of course tempting just to examine mapped routes retrospectively, and attribute decisions to the points where the travel direction changed most strikingly. Human vision is exquisitely sophisticated at shape recognition; unfortunately, the human brain is notoriously poor at assessing statistical significance. Therefore, while the eye may be good at detecting potential changes of direction, the brain is very bad at assessing whether or not these apparent changes are so pronounced as to be statistically significant. Thus the use of a sound statistical technique is essential, and thus at present most animal researchers (rightly) make little use of mapped travel routes.

Our aim in this paper is to introduce a method that can enable researchers to begin to go beyond intuitions and assumptions about where and when travel decisions are made, by applying statistical assessment as a critical first step in interpreting an animal's route choices. The method is based on identifying, to a pre-set margin of certainty, those *change-points* at which a travelling animal or group of animals changes direction. We therefore term the statistical procedure involved the *Change-Point Test* (CPT). The CPT offers the chance to identify where and when changes of direction occur, independently of the possible reasons for the change, the animal's demeanour at the change-point, and any resources to which the travel led. Inevitably, reliable identification of change-points will be hindered by extraneous factors causing animals' routes to deviate, including distractions from their physical and social environment. Thus the detection of a change-point must be viewed in signal detection terms (Green and Swets 1966), a matter of picking out a real signal against a noisy background. Judgement will be required on how the method should be applied and what level of statistical significance to accept; and these judgements may vary according to the scale and pattern of travel of the particular species under study. This may seem inferior to the conventional certainties of testing at pre-specified significance levels guided by power calculations, but we would suggest that those certainties are often chimeras, and the effort of tailoring a statistical test to a particular situation may be revealing in itself. More fundamentally, we emphasize that significant results from the CPT are only the starting point for understanding the behaviour. Animals may change direction merely because of the lie of the land, perhaps meeting an impenetrable barrier or the edge of suitable habitat, and in any case straight-line travel does not necessarily imply foreknowledge of some goal at its endpoint. To distinguish these possibilities, other data will need to be combined with the CPT results.

We evaluate the behaviour of the CPT first with 'synthetic data', artificial paths in which different levels of random movement have been superimposed on linear routes that do or do not include a clear change of direction. The aim is to determine how well the CPT does in detecting underlying change-points and

avoiding false positives. Then we apply the CPT to actual ranging data of two primate species that exhibit contrasting foraging patterns. We use data from baboons that forage as a cohesive group from a single central sleeping site, over a range shared with many other groups; and from chimpanzees, that make their own sleeping nests and are thus able to travel in an unrestricted way within their exclusive territory. This choice of non-human primates as a test-bed for the CPT is a purely practical one. To evaluate the test, detailed ranging data of individually known animals is required. In many primate studies, including our own, ranging data is collected by an observer following a known individual or group on the ground: this means that GPS data describing individuals' travel routes can be obtained straightforwardly. At present, such data are relatively scarce for many species of animals. However, once the utility of the CPT is established, we hope that investigators of a much wider range of animal species will find it worthwhile to gather and analyse data of this kind.

Introduction to the Change-Point Test (CPT) and its evaluation

The CPT can be applied whenever an animal's travel path has been accurately represented as a series of physical locations, called *waypoints*. Although it is not required in order to apply the CPT, samples would normally be taken at a regular rate. The rate of sampling will determine the scale at which the CPT analyses the animal's path. In the data used to illustrate the CPT in this paper, instantaneous sampling at fixed intervals of a few minutes was used; however, for other species, sampling every few seconds or hours may be more appropriate. Travel between each consecutive pair of sample locations is represented as a *vector*.

In essence, the CPT examines whether the vectors representing the path after a given point are aligned with those before it; in other words, did a change of direction occur there? This very general procedure has a range of potential uses in biology, but in this paper we shall illustrate its operation when applied to the specific question that has been our particular concern. Like many field researchers who trace the travel paths of their study animals, we often observed an animal

spending time at a particular place, engaged in activity that might very plausibly have been its reason for going there. To evaluate the significance of the location for the animal itself, however, the critical first step is to discover whether, and for how long, the animal had been headed towards that site before it arrived. We have used the CPT to provide an objective estimate of the extent of such 'directed' travel. In this case, the CPT must be applied 'backwards in time', starting from locations which might have been the goals of deliberate travel (see Fig. 1).

Identifying potential travel goals — quantifying the potential value of resources for a species — could be a major exercise in itself. We followed White and Wrangham (1988) in using the simple heuristic of equating time-spent with value: for each study population, we set a critical value of time-spent to define a potential goal of travel. As with the use of any criterion, some data will inevitably be misinterpreted. Too strict a level (i.e. too long a wait) and many potential foraging goals will be missed, too lax a level and brief pauses in travel may be confused with ecologically relevant behaviour. In practice, we found that the extent of this problem varied with species. In chimpanzees, varying the threshold from 20 min to 60 min made essentially no difference to the locations identified as potential goals; for baboons, a threshold as low as 2 min missed a significant amount of food ingestion. Even with perfect foreknowledge and cognitive mapping skills, it would be unreasonable to expect an animal always to allot its travel time perfectly. Some 'mistakes' are inevitable. For instance, the resource may have been depleted by a competitor of the same or another species since it was last visited. In such cases, rigidly insisting upon a criterion of a certain time-spent would risk failure to detect an authentic goal. As our focus was on cognitive competence rather than ecological efficiency, we treated all change-points discovered by the CPT as potential goals for previous travel, even if they were not coincident with appreciable time-spent at the locations. The reasonableness of this approach can be examined empirically by asking whether, in fact, most change-points are coincident with real resources, as compared to control data, i.e. sites chosen at random. (Additionally, it might be the

case that change-points were situated at prominent landmarks that aided further locomotion, a possibility that could also be investigated empirically.)

Typically, then, we examined a recorded day's travel path by applying the CPT sequentially to segments of travel 'backwards in time' towards the place at which our subject(s) spent the previous night, until a change-point was discovered (see Fig. 2). This location then became the starting point for applying the CPT again. Each time it is applied, the CPT compares a set of vectors on one side of a possible change-point with a set of vectors on the other. We label the k vectors describing travel after a potential change-point $v_1,...,v_k$, with vector v_1 leading to the potential goal location, v_2 leading to v_1 and so on. Similarly, the q vectors describing travel before the potential change-point are labelled $v_{k+1},...,v_{k+q}$, with v_{k+1} leading to the putative change-point, v_{k+2} leading to v_{k+1}, and so on, as explained in Fig. 2. If the two resultant vectors $v_k+...+v_1$ and $v_{k+q}+...+v_{k+1}$ are found to be collinear then the test is then applied again at the next point, backwards along the travel path. When the two resultant vectors depart from collinearity at the pre-set level of significance, a change-point is identified.

Investigation of whether or not a given waypoint can reasonably be regarded as a change point proceeds in two stages: (i) measuring the lack of collinearity of the vectors $v_k+...+v_1$ and $v_{k+q}+...+v_{k+1}$, (ii) assessing whether or not this lack of collinearity is statistically significant. Lack of collinearity of $v_k+...+v_1$ and $v_{k+q}+...+v_{k+1}$ is measured by comparing the lengths, R_k and R_q, of $v_k+...+v_1$ and $v_{k+q}+...+v_{k+1}$ with the length, R_{k+q}, of the resultant of $v_{k+q}+...+v_1$ (see Fig. 2). The intuitive idea is that, if the point where v_{k+1} meets v_k is not a change-point then $v_k+...+v_1$ and $v_{k+q}+...+v_{k+1}$ are almost collinear and so R_{k+q} will be approximately equal to R_k+R_q. In contrast, if there is a change-point where v_{k+1} meets v_k then R_{k+q} will be appreciably less than R_k+R_q. The test statistic, $R_k+R_q-R_{k+q}$, measures the discrepancy from collinearity. Assessment of the statistical significance of the value of $R_k+R_q-R_{k+q}$ (i.e. the extent to which its value is 'surprisingly large') is carried out

by a permutation test. The test regards the observed value of $R_k + R_q - R_{k+q}$ as significant if this value is among the largest (e.g. among the top 1% for a test at the 1% significance level) of the values that would arise from changing the order of the vectors $v_1,...,v_{k+q}$ (so that, in general, a different set of k of the $k+q$ vectors is regarded as describing travel after the waypoint). More details are given in the mathematical description of the CPT below. The advantage of the permutation test, over tests based e.g. on normal distributions, is that it is not necessary to make any (possibly unrealistic) assumptions about the distributions of the random vectors $v_1,...,v_{k+q}$.

The risk of failing to detect a genuine change-point is highest at small values of k and the number q of vectors included in $v_{k+1},...,v_{k+q}$ will also change the test's sensitivity (i.e. its power). Indeed, in practice, a change-point only one vector away from a potential goal (that is, $k=1$) would be almost undetectable when q is small. However, as will become clear in the examples below, using the largest possible set of vectors $v_{k+1},...,v_{k+q}$ is not necessarily advantageous, and the appropriate balance between power and precision needs to be decided for the problem under investigation. In the case studies that follow, we aim to illustrate how, in practical cases, appropriate values of q may be chosen; how a change-point may best be identified if there remains ambiguity from applying the CPT; and what difficulties need to be borne in mind when using the CPT.

Mathematical description of the CPT

The directions of the vectors $v_1,...,v_n$ can be specified by the angles $\theta_1,...,\theta_n$ that they make with some fixed reference direction, e.g. north. In order to be able to assess statistically the existence and location of change-points, we assume that $\theta_1,...,\theta_n$ are observations on independent random angles which have population mean angles $\mu_1,...,\mu_n$ (see Mardia and Jupp 2000, §3.4.2). The null hypothesis, that there is no change-point, is

$$H_0 : \mu_1 = ... = \mu_n .$$

The alternative hypotheses that the first (going 'backwards in time') change-point is at k $(k = 1,...,n-1)$ are

$$H_k : \mu_1 = ... = \mu_k \neq \mu_{k+1}.$$

The geometrical argument given in the informal overview of the CPT above indicates that it is appropriate to reject H_0 in favour of H_k if $R_k + R_q - R_{k+q}$ is 'large', where

$$R_k = \| v_k + ... + v_1 \|,$$
$$R_q = \| v_{k+q} + ... + v_{k+1} \|,$$
$$R_{k+q} = \| v_{k+q} + ... + v_1 \|.$$

In the special case in which $v_1,...,v_n$ have the same length, the statistic $R_k + R_q - R_{k+q}$ is the basis of the two-sample Watson–Williams test (Batschelet 1981, §6.2; Mardia and Jupp 2000, §7.3.1) for equality of two probability distributions on the circle.

In order to avoid (a) making assumptions about the distributions of the angles $\theta_1,...,\theta_n$, (b) complicated distribution theory, it is appropriate to assess the significance (or, equivalently, the 'largeness') of $R_k + R_q - R_{k+q}$ by using a permutation test. (Permutation tests, known also as 'randomisation tests', are described in many books on non-parametric statistics. Our test is in the spirit of the usual 2-sample permutation test, as described on pp. 360–364 of Conover 1971.) Our permutation test is based on the fact that if H_0 is true then all $(k+q)!$ values of $R_k + R_q - R_{k+q}$ obtained by permuting $v_1,...,v_{k+q}$ are equally probable. Thus the significance of the observed value of $R_k + R_q - R_{k+q}$ can be assessed by comparing it with the $(k+q)!$ values obtained by permutation. In principle, the permutation test of H_0 versus H_k proceeds as follows:

(a) For each permutation σ of $1,2,...,k+q$, put

$$R_k(\sigma) = \| v_{\sigma(k)} + ... + v_{\sigma(1)} \|,$$
$$R_q(\sigma) = \| v_{\sigma(k+q)} + ... + v_{\sigma(k+1)} \|,$$
$$R_{k+q}(\sigma) = \| v_{\sigma(k+q)} + ... + v_{\sigma(1)} \|;$$

(b) arrange the list of $(k+q)!$ values of $R_k(\sigma) + R_q(\sigma) - R_{k+q}(\sigma)$ into numerical order;

(c) if the observed value of $R_k + R_q - R_{k+q}$ is the rth largest in the list then the P-value is $r/(k+q)!$.

In practice, since $(k+q)!$ is usually too large for listing all permutations to be feasible, a random set of N permutations is used and the P-value is taken as r/N. The randomness of the set of permutations used means that repeating the test on the same data set will result in a slightly different value of r/N. If N is large then such fluctuations in r/N are negligible. For example, if $N = 1000$ and the true P-value is at most 0.1 then r/N is almost certainly within 0.02 of the true P-value.

The null hypothesis, H_0, is tested in turn against $H_1, H_2, \ldots$. The first change-point is estimated as the first value of k for which H_0 is rejected in favour of H_k. Note that, since (a) several tests are being carried out, (b) there is overlap between the portions of the data used in these tests, it is difficult to calculate the significance level of the combined test. Once the first change-point has been identified, the second change-point is estimated by taking the first change-point to be the new putative goal and applying the above procedure to the portion of the path leading to that. Repeating this procedure identifies subsequent ('backwards in time') change-points.

Code in R for performing the Change-Point Test is available from **http://www.mcs.st-andrews.ac.uk/~pej/CPT.html**.

Evaluation of CPT with synthetic data

We created eight artificial routes to examine the CPT's performance on a small set of data with known properties (see Fig. 3). Routes a, b, c and d were intended to be noisy versions of broken straight routes that contained a change-point at waypoint 12. Here, as in all subsequent discussion, we label waypoints sequentially from the start of the day's travel, and use a variable t to count the waypoints 'backwards' from the point at which the CPT is first applied, for example the end of a day's travel. Thus, $t = 0$ at the end of a day's travel and $t = k$ at the first (backwards, from

the end of the day's route) potential change-point considered by the CPT. In these synthetic routes, where 'travel' begins at the left and ends at the right of the figures, waypoint 12 corresponds to $k = t = 13$, when working back from the end of the route. Each vector was generated using a random step length R and a random angle θ. R was taken from a Normal distribution with a mean of 1 and a standard deviation of 0.1. θ was taken from a von Mises distribution (Batschelet 1981, §15.3; Mardia and Jupp 2000, §3.5.4), with a mean direction of 0° for the vectors 1 to 12 (shown towards the left in each of the panels a-d), and with a mean direction of 45° for the vectors 13 to 25. The concentration parameter κ was 100 for route a, 10 for route b, 3 for route c and 1 for route d; thus the noise background increased from the lowest level in route a to the highest in route d.

In contrast, routes e, f, g and h were intended to be noisy versions of straight routes, with no real change-points. Again, R was taken from a Normal distribution with a mean of 1 and a standard deviation of 0.1. θ was taken from a von Mises distribution with mean direction 0° and a concentration parameter $\kappa = 100$ for route e, $\kappa = 10$ for route f, $\kappa = 3$ for route g and $\kappa = 1$ for route h. In signal detection terms, route e matches route a in its level of noise (N), but differs in lack of a signal (S); correspondingly, f matches b, g matches c and h matches d. The task of the CPT is to locate the signal ('successful detection') in most cases of S+N, without an undue number of 'false positives' for N alone.

We ran six variants of the test on each of these routes, with $q = 1,2,...,6$, and viewed as the change-point the first value of k that was significant, for two significance levels, $\alpha = 0.05$ and $\alpha = 0.01$. The CPT was applied from $t = 0$, located as the rightmost point on each of panels a-h.

For route a, the S+N route with the lowest level of noise, the results of all variants with $q > 1$ agreed, detecting a significant directional change close to the true value of $t = 13$ at $\alpha = 0.01$ in all cases. Note that, because of the inclusion of more vectors after the point under examination, the point identified as the change-point tends to 'creep' forwards: in this case, $t = 13$ for $q = 2$, but $t = 12$ for $q = 3$ and 4, and

$t = 11$ for $q = 5$ and 6. With $q = 1$, the statistic reached significance only at $\alpha = 0.05$, and then at an incorrect location, $t = 15$; however, using $\alpha = 0.05$ produced no false positives at any other choice of q. For the corresponding lowest-noise N route e, all variants correctly detected no change-point, when using $\alpha = 0.01$. However, when using $\alpha = 0.05$, a false positive was found at with $q = 1$, at $t = 14$, and with $q = 6$, at $t = 18$.

At a slightly higher level of noise, in the S+N route b, the CPT remained robust to variation in the value of q. All variants of the test with $q > 1$ identified $t = 13$ as the only change-point in this route, at both $\alpha = 0.01$ and $\alpha = 0.05$. (The lower level of evidence required at $\alpha = 0.05$ allowed the statistic to attain significance at $t = 12$ for variants $q = 5$, $q = 6$, showing a slight 'creep' forwards.) In contrast, the variant with $q = 1$ failed to identify any directional changes at all, even with $\alpha = 0.05$, suggesting that this variant is seldom likely to be useful. For the corresponding N route f, the all variants ($q = 1,2,...,6$) correctly detected no change-point when using $\alpha = 0.01$. However, with $\alpha = 0.05$ false positives were found at $t = 12$ (with $q = 2$ and $q = 4$) or $t = 11$ (with $q = 3$ and $q = 5$).

At the next highest level of noise, in the S+N route c, a change-point at $t = 13$ was picked out by test variants with $q = 4$ or $q = 5$; with $q = 6$, a change-point of $t = 14$ was found. In all these cases, detecting change-points relied on using $\alpha = 0.05$; at $\alpha = 0.01$, no change-points were found. Variants with $q = 2$ and $q = 3$ found the first directional change at $t = 5$, but when these were restarted at $t = 5$, they both found the true change-point at $t = 13$. Thus, test variants $q = 2,3,4$ and 5 (and arguably 6) all identified the 'true' change-point, but versions $q = 2$ and $q = 3$ also picked up a false positive change-point. Using $q = 1$ again produced no evidence of the change-point, even at $\alpha = 0.05$. For the corresponding N route g, none of the variants found any directional changes, whether using $\alpha = 0.01$ or $\alpha = 0.05$.

At the most extreme level of noise we examined, in the S+N route d, false positives were found with all variants of the test $q = 1,...,6$ when using $\alpha = 0.05$ (at

$t = 18, 7, 6, 6, 5, 5$, respectively; the last just reached significance at $\alpha = 0.01$, whereas no change-points were detected at $\alpha = 0.01$ with other variants). Moreover, only variants $q = 3$, $q = 4$ detected the 'true' change point at $t = 13$ when they were restarted from an earlier false positive location. False positives were also a feature of using the CPT with the corresponding N route h. Variants with $q = 1, 2, 3$ all detected false positive change-points at $\alpha = 0.05$ (at $t = 13, 6$ and 5 respectively). Only the test variants with high values of q correctly detected no change-point on the artificially generated route.

Overall, we found the CPT to be useful in identifying the artificially-generated change-point in all but the noisiest route, provided values of $q > 1$ were used. The variant with $q = 1$ was next-to-useless over the relatively short spans we tested. With much larger values of k (i.e. routes in which change-points are typically much more than 13 waypoints apart), even that variant might prove valuable. However, deciding upon the most appropriate value of P may depend on the characteristic properties of the routes under test. At the $\alpha = 0.05$ level of significance, all values of q were prone to giving false positives, that is, identifying change-points when none were actually present. At the 0.01 level of significance, no false positives were found in any route, but the true change-point was missed against moderate noise. In this case, using $\alpha = 0.05$ was more successful: no false positives were found in the absence of a signal, and the signal of the change-point was correctly detected with all values of $q > 1$. However, in two cases, a false positive initially obscured the true change point, which was only detected when the test was re-run from the false positive. Evidently, and as might be expected from theoretical considerations, there is a trade-off between the rates of correct detections and false alarms, and choice of significance level (α) must be made according to the goals of researchers. With the highest level of noise we investigated, the CPT was not successful in detecting true change-points from random noise.

Case study 1: Baboons in dry woodland

Baboons are terrestrial primates found in the African subcontinent between the Sahara and Cape of Good Hope. They live and range in cohesive groups of several males, several females and their offspring; group sizes vary dramatically across habitats and subpopulations. It is believed that certain individuals within a baboon group are more influential than others in deciding where to go, but only in the case of unusually small groups has the identity of the animal(s) leading a group been discovered (Byrne et al. 1989; Kummer 1968). Thus, a baboon group's foraging route must be viewed as resulting from the decisions of a single entity.

Most baboon groups utilize a number of sleeping sites, but the group whose data are employed here returned to the same sleeping site every night during the 16 months, from May 2001 to August 2002, that we studied them (Noser 2004). We followed this group of 25 Chacma baboons *(Papio ursinus)* at Blouberg Nature Reserve, South Africa (22°58' S / 29°09' E) on foot throughout whole days. On average, they travelled 7.7 ± 2.1 km per day within their home range of 13.5 km^2 woodland savannah. We recorded the group's position at regularly spaced time intervals of 5 min by means of a GPS receiver (see Noser and Byrne 2007, for details on data collection procedure).

As feeding generalists, baboons rely on a wide variety of plant food sources, and to a lesser extent also on insects, reptiles and small mammals. Yet baboon feeding is highly selective (Altmann and Altmann 1970; Whiten et al. 1987): among thousands of plant species within their home range, a baboon group may use only a hundred species, and use only certain parts of each (e.g. only young leaves, only roots etc). Baboons constantly scan the ground for food and pick up and ingest small items while walking. It is therefore presumed that much of their food is found by visual search, on the way to more important and probably larger resources to which travel is directed. To identify potentially important resources, we used a criterion that at least three animals should exploit a resource patch simultaneously for 2 min or longer. Visits to waterholes were scored when the majority of group

members drank. Where movement came to a halt for longer than 5 min but neither feeding nor drinking met these criteria, we scored the locations as 'unknown resource'; this category may include cases where the baboons perceived a threat from predation or another baboon group. In addition, we viewed the sleeping site as an important resource (Noser and Byrne 2007).

The baboons' ranging differed strikingly between the dry season, when food in the woodland savannah was generally scarce, and the rainy season, when food was abundant. During the dry season, ranging was directed over large distances towards distant fruit sources and water holes (Fig. 4, top left and bottom right panel). In contrast, they moved in a less directed manner and over shorter distances during the wet season (Fig. 4, remaining panels), opportunistically feeding on a wide variety on fruit, flowers and seeds (Noser and Byrne 2007a and b).

In order to evaluate the CPT for baboon ranging, and in particular to find the most appropriate values of q and the nominal significance level α, we applied the CPT to each of the four routes shown in Fig. 4. We performed a total of 192 iterations of the CPT with $q = 1,2,...,10$. The iterations were run independently: only change-points identified for that specific value of q were used as end points in the next iteration of the test. By doing so, we took it that the most useful value of q would be the one maximally sensitive to directional changes. That is, the optimum value of q should allow detection of the largest number of change-points per route.

In choosing the appropriate significance level, there is trade-off between statistical robustness of the results on one hand and the number of locations identified as change-points on the other. Thus, non-stringent significance levels (e.g. $\alpha = 0.1$) increase the amount of potentially important information about the animals' spatial decisions, but this information is based on weaker statistical evidence. Since we aimed to give statistical robustness high priority, especially in the light of the CPT's implicit multiple testing, we favoured a stringent level of significance. For baboons, we found that a significance level of $\alpha = 0.01$ identified a sufficient number of change-points for evaluation.

We first examine in detail the results of a single iteration of the test, during its application to a dry season route (i.e. Fig. 4, top left panel), for all values of q that we considered (Fig. 5). This iteration started at $t = 0$, which corresponds to the sleeping site, and thus was presumed the last goal location of that day's ranging. The order in which the waypoints were used in the CPT is indicated by the arrow in each panel of Fig. 4. (Recall that, for the first iteration of the CPT on a given day, the value of t at the first potential change-point is $t = k$. For all subsequent iterations, the value of t at a potential change-point is $t = k + t_0$, where t_0 is the value of t at the start of that iteration. In Fig. 5, we show only the first iteration of the test. Therefore, k in Fig. 5 corresponds to t in Fig. 4.) It is useful when running the CPT to produce (as our code does), plots of $-\log P$ against k, where P denotes the corresponding P-value. For testing at nominal significance level α and for given values of q and k, the waypoint is considered to be a change-point if $P < \alpha$, i.e. if the plot of $-\log P$ at k lies above the horizontal line corresponding to $-\log \alpha$. As Fig. 5 shows, with $q = 1$ the test was least sensitive to directional changes: a significant directional change was found only at $t = 52$ with $\alpha = 0.05$. In contrast, a change-point was found at $t = 14$ with $q = 2$, and at $t = 7$ with $q = 3$. Using $q = 4$ and $q = 5$ resulted in a similar pattern: both curves peaked at $t = 6$. However, $-\log P$ was greater than $-\log \alpha$ at $k = 5$ with $q = 4$, but not with $q = 5$. Thus, the variant with $q = 4$ indicated a change-point at $t = 5$, and the variant with $q = 5$ at $t = 6$. The variants with $q = 6$ and $q = 7$ both suggested that there was a directional change at $t = 4$, whereas $q = 8$ and $q = 10$ found a change-point at $t = 3$.

As this small evaluation confirms, the test is relatively insensitive even to pronounced directional changes when using very low values of q: this effect is most obvious with $q = 1$. For example, the variant with $q = 1$ did not find a single change-point in one of the wet season routes (Fig. 4, top right panel), although variants with higher values of q did. Results become more consistent with increasing q.

The slightly different results of the variants with $q = 6$ to $q = 10$ (Fig. 5) do not reflect any real difference in sensitivity of test variants, but rather illustrate an

inevitable tendency of the test to 'look around the corner'. A single outlier in a large segment of q vectors (say one out of ten) tends to have less weight than an outlier in a segment containing only a few vectors (e.g. one out of three or four). Thus, variants with high values of q tend to react too early, and may indicate significant directional changes a few locations ahead of the 'true' change-points. Consequently, the more vectors we include in the 'reference' segment of q vectors, the more we risk missing the exact change-point by a location or two. In such cases, we can take advantage of the fact that several consecutive values of - log P in a row exceed their critical values (e.g. Fig. 5, variants with $q = 6, 7, 8$ and 10). The 'true' change-point may then be found by considering not just the first value of - log P that exceeds the critical value, but also consecutive subsequent ones that exceed the critical value. The value of k giving the largest of these values (thus forming the peak of the line) can be viewed as the change-point. When using this 'peak rule' to read Fig. 5, the variants with $q = 6, 7, 8$ and 10 agree: they all find a significant directional change at $t = 5$. This suggests that the CPT, applied to baboon ranging data, is robust to the choice of q – provided q is relatively high.

To assess the generality of this conclusion, we extended this analysis to all four baboon routes, using the CPT to examine each whole day's travel. The cumulative number of change-points found in this way increased as q increased from 1 to 6, but then decreased with higher values of q (see Fig. 6). A partial explanation that we can offer for this is the fact that when q gets very large, the corresponding segments are likely to include more and conflicting directional changes. As a result, the sensitivity to directional change from the segment based on k vectors decreases. On the other hand, the length of the segment based on q vectors delimits testing of vectors that occur in the vicinity of the starting point of the animals' journeys: the larger q is, the further away from the journey's start are the locations that can be tested at all. Therefore, an intermediate q seems to be most appropriate, and for our baboons' ranging we suggest a value of $q = 6$ to be

optimal. Fig. 4 shows the test results corresponding to $q = 6$ and $P < 0.01$ in the four baboon routes, with the stars indicating the change-points.

In order to examine whether these findings are supported by independent evidence, we investigated both topographical features and the baboons' behaviour at each of the change-points of each route. We discuss the animals' behaviour in chronological order, that is, in the opposite direction to that used in testing the corresponding ranging data. As a detailed illustration, we first discuss a route that was recorded towards the end of the dry season (top left panel of Fig. 4). The first change-point of that journey corresponded with the area where a thicket began, and the animals started to follow a narrow trail leading to a water hole. The water hole itself was situated two waypoints further on. The second change-point was situated one waypoint after that water hole, when the animals started to head at high speed towards the main feeding area of that day. The third and fourth change-points occurred at two Marula trees *(Sclerocarya birrea)* in that feeding area, where the animals fed on an unidentified epiphyte for 35 and 13 min respectively. Furthermore, we recorded a bout of aggressive social behaviour at the location of the next change-point. In this, the alpha male gave a so-called 'roar-grunt' and chased his females. Such behaviour occurred relatively seldom in our study group, but observations of other instances suggested that it occurred when the females and young seemed to aim at other places than the alpha male. The next change-point in the top left panel of Fig. 4 coincided with the arrival of the study group at the border of an abandoned crop field; they then followed this border until reaching the water hole. Two of the remaining three change-points of that day indicate feeding trees, a knob-thorn acacia *(Acacia nigrescens)* and a star-chestnut *(Sterculia rogersii),* but the last change-point was not associated with any particular behavioural or topographical features.

Extending this analysis to all four baboon routes, we found that the 29 change-points identified were associated with highly interpretable events in 25 cases. These concerned feeding in 16 cases, drinking in 4 cases, disruptions of the journey in 2 cases (an intergroup encounter, a car driving by), topographical

features in 2 cases, and social behaviour in 1 case (see above for explanations of the latter two). In order to test whether the association of change-points with interpretable events was more than coincidence, we picked a set of waypoint locations at random along the same routes, one location in each segment of travel between change-points. Baboons were more likely to be feeding, drinking or to be in close proximity to another baboon group at change-points, compared to randomly chosen locations where they were more likely to be travelling or resting (Fisher's exact test $P = 0.0005$). At random waypoints, baboons were travelling or resting in 75% of cases, compared to only 24% at cases identified as change-points. Thus the change-points detected by the CPT were closely linked to the study animals' behaviour, measured independently; we conclude that the results of the test are indeed meaningful for baboon travel.

Case study 2: Chimpanzees in moist tropical forest

Chimpanzees (*Pan troglodytes*) are large-bodied apes found in the forests and woodlands of equatorial Africa. They are primarily fruit-eaters, although their varied diets include other plant parts as well as insects, small mammals and even monkeys. Chimpanzees live in communities of up to 100 individuals, using a common territory from which outsiders are actively excluded. Within a community, individuals separate off to form temporary parties that can vary in size from one to tens of chimpanzees. Any one party can persist for a few minutes to many hours; membership is fluid and individuals frequently change who they are with; hence the social organisation is commonly labelled 'fusion-fission'. Moreover, individuals can and do range entirely alone on occasion: thus each chimpanzee's ranging, whether alone or with others, can be considered as resulting from its own decision-making.

We studied chimpanzees inhabiting the moist tropical forest of the Budongo Forest Reserve, Uganda. Here, members of the Budongo Forest Project (www.budongo.org) have studied the Sonso chimpanzee community continuously since 1990. Individuals are well habituated to human observation at distances of five metres or more. The chimpanzee community consisted of between 53 and 62

chimpanzees during the study period (September 2002 – September 2003), and occupied a home range of approximately 7 km^2 (Newton-Fisher 2003).
In contrast to the baboons we studied (above), chimpanzees are not central place foragers: they do not return to the same site each night, or even to a restricted set of sites. Instead, chimpanzees can sleep almost anywhere within their home range because they construct their own night nests (Goodall 1986). Chimpanzee sleeping-sites therefore do not necessarily represent the termination of a planned travel route. For this reason, we extended the time periods over which we analysed ranging behaviour. One target adult chimpanzee was followed continuously for two days, from when it rose from its nest at dawn on the first day to when it nested again at dusk on the second day (mean total route length 5.7 km across the two-day focal period). Throughout each focal sample, the location ('waypoint') of the target individual was recorded every five minutes using a GPS device, and concurrent behavioural data detailing the activity of the target animal was recorded continuously.

Like baboons, chimpanzees spend most of their travel time on the ground: although they often remain arboreal when moving *within* food patches, they move *between* resources almost exclusively terrestrially. Unlike baboons, chimpanzees rarely feed whilst travelling on the ground, instead making definite and prolonged stops, often for over an hour. At each stop, chimpanzees may feed, drink, engage in social interactions, or rest (i.e. periods of sleep or inactivity where no obvious activity is noted). During the study, very few stops of less than 20 minutes were recorded for any of these purposes, so this interval was used as the criterion for defining a potentially important resource.

Here, we apply the CPT to two-day travel routes made by four adult male chimpanzees (Fig. 7). Each route was examined with six variants of the CPT; $q = 1,2,3,4,5$ and 6. As with the analysis of baboon travel, the variants were run independently. That is, only change-points identified by a particular value of q were used as starting points for the next iteration of the test with the same value of q, and the CPT was applied until all change-points along the whole route had been

identified. For all the chimpanzee routes presented here, we used $\alpha = 0.05$. (At $\alpha = 0.01$, too few change-points were identified for evaluation.)

For illustration (Fig. 8), we present the results with all six values of q for the first iteration of the test, as applied to the chimpanzee route shown in the top left panel of Fig. 7. This iteration started at the final recorded waypoint of the two-day route, labelled as $t = 0$. With $q = 1$, the CPT did not detect a change-point until $t = 34$. With $q = 2$, $t = 10$ was the first point at which the criterion was reached; however, the peak rule, described above, would suggest that the actual change-point occurred at $t = 11$. With $q = 3$, the first point at which the criterion was reached occurred at $t = 6$, although a second peak at $t = 10$ was significant at $\alpha = 0.01$. At $q = 4$ and 5, the first significant peak occurred at $t = 10$, and with $q = 6$ the first significant peak was at $t = 9$, again using the peak rule.

From this example it is already evident that the relatively insensitive $q = 1$ variant of the CPT is unlikely to be a useful value for examining forest-dwelling chimpanzee ranging patterns. Furthermore, the high value $q = 6$ brings an inevitable tendency to indicate change-points earlier than the true values, as we noted when examining baboon ranging. The cumulative number of change-points found over the four chimpanzee routes increased with q, up to the value $q = 4$, and then declined (Fig. 9). Thus, for these routes, $q = 4$ is the most powerful variant of the test, detecting the greatest number of change-points across the four test routes. The locations of all change-points identified across the four routes with the variant $q = 4$, $\alpha = 0.05$ of the CPT are indicated on Fig. 7.

To assess whether the change-points detected reflect events that held meaning for the chimpanzees, we examined their activity at these points. Using the same route as an exemplar (top left panel of Fig. 7), we discuss the changes of direction along this route in chronological order, starting from the first waypoint recorded at the start of the two-day sample. The first change-point identified at waypoint 8 ($t = 50$) coincided with the focal subject (MA) and his party fusing with another party of males and a sexually receptive female. They did not stop at this

waypoint, but after joining together all moved north, subsequently stopping three waypoints further on to feed together for 30 minutes. The next change-point identified, however, occurred 5 min after leaving this feeding site, at waypoint 12 ($t = 46$). This may simply reflect a slight lack of precision associated with values of q greater than one, but in fact this waypoint occurred just after pant hoots (long-distance vocalisations) were heard in the distance. It may therefore have been this auditory stimulus rather than any food resource that affected the subject's behaviour.

The focal subject and party next changed direction at waypoint 17 ($t = 41$). Between this and the next change-point at waypoint 24 ($t = 34$), MA and his party stopped twice for at least 20 minutes each time to feed and socialise, but neither of these stops was identified as a change-point. At the next change-point, waypoint 24, MA rested and socialised on the ground with the other males in the party for 24 minutes. He then set off in a new direction, travelling the short distance towards waypoint 26 where the party nested for the night. This location was not identified as a change-point, since the following day MA continued to move generally west, until the change-point at waypoint 36 ($t = 22$), where he fed for 27 minutes with other males. Pant hoot vocalisations were heard from the south shortly before MA and party moved away from this feeding tree. MA travelled south to the next change-point at waypoint 44 ($t = 14$), where he stopped to feed and socialise with other males for 59 minutes. At the next change-point, waypoint 48 ($t = 10$), MA fed only for 19 minutes, just under the time chosen to indicate an important resource. Once again, MA and his party left this feeding resource shortly after pant hoots were heard from the south, and he continued to move broadly south, until the end of the route at waypoint 58 ($t = 0$). Here, the point from which analysis with the CPT began, he fused with other chimpanzees, fed and socialised for over an hour, and eventually nested for the night.

Adding these results to similar analyses on the remaining three chimpanzee routes, we found that the 26 change-points identified were associated with interpretable events in at least 20 cases. These incorporated important food

resources in 12 cases, social fusions with others in five cases (one whilst moving, and four before stopping to groom, feed or rest), and hearing pant hoots in the same direction as the subsequent travel in three cases. Of the remaining six change-points, four were associated with the party stopping to rest (twice, when stopping for the night and once four minutes before; once, when stopping to rest, groom and socialise for at least 20 minutes during day travel), and one occurred at a waypoint two minutes before turning sharply and stopping to feed on a large tree for 23 minutes. The final waypoint (waypoint 17 in the above exemplar) was not associated with any obvious behaviour: an almost 90^0 turn occurred while the target animal was moving. The mean time spent at change-point stops was 40 min (±43 min SD, excluding night nesting sites).

In order to examine whether the association of change points with events was merely coincidental, we compared the activity and the time spent at each of the 26 change point locations with those at 26 other waypoints randomly selected across the four routes. Chimpanzees spent longer at change-point locations than random waypoints (74 min compared to 14 min; $t = 2.4$, df$= 46$, $P = 0.021$, excluding the two nest sites and two corresponding random points). Chimpanzees were more likely to be engaged in feeding activity, fusion of two parties or hearing pant-hoots from a separated party at change-points compared to random waypoints; conversely, travel, resting or nesting activity was more common at random points (Fisher's exact test, $P = 0.0001$). At random waypoints, baboons were travelling or resting in 77% of cases, compared to only 27% at cases identified as change-points. We therefore suggest that the change-points detected in chimpanzee ranging by this statistical tool were indeed meaningful.

Summary

Our restricted explorations clearly cannot exhaust the issues that might arise in using the change-point test to best advantage. Nevertheless, by choosing species whose ranging varies in several ways, we believe we have shown that a uniform

approach can be applied quite broadly. The real-world examples used here, chimpanzees and baboons, differ in how their travel is constrained (returning daily to a single sleeping site, vs. unrestricted sleeping sites), in spatial distribution (overlapping range vs. territoriality), in habitat (dry woodland vs. moist forest), and in foraging configurations (cohesive group vs. fission-fusion). In both cases the CPT was successful in identifying a series of places at which travel direction changed towards locations that – in the great majority of cases – were readily interpreted in biological terms.

We propose that using the CPT should generally include the following stages:

1. **Delimit the problem**. As with any research study, the question to which the CPT is to be applied will affect how data are collected, and this needs to be fixed first. The resolution with which a travel route is tracked depends on the rate of sampling of physical locations ('waypoints' if GPS is used): the appropriate rate can be expected to vary with a species' size and nature of foraging. Similarly, the most useful criteria with which to define the potential goals of travel will be a function of local factors and the researcher's own goals. This applies whether these possible goals are identified by using the subjects' own behaviour (time spent, activity engaged, directional change), or by independent human estimation of resource value at each location.

2. **Choose optimal values of** q. The CPT is in fact a family of tests, varying in the number (q) of vectors before each putative change-point which are compared with the k vectors after it. Ideally, this process of choice should replicate the sort of analyses we have carried out for baboons and chimpanzees in this paper. Two competing trends define a likely optimum value of q, for any particular case.

Firstly, there is the obvious point that the power of a test increases as more data are included. Very low values of q thus risk missing genuine change-points in travel. For both baboon and chimpanzee travel, we found that $q=1$ systematically failed to detect many change-points that were revealed clearly by higher values of q. The reality of these 'missed' change-points was shown for

$q \geq 2$, often by a clear peak in a series of consecutive highly significant values of - log P, not merely a single, potentially rogue value, and a high level of significance. Moreover, with synthetic data that imposed random variation on routes with definite change-points, the CPT with $q = 1$ failed to detect most change-points. With $q = 1$, the CPT simply does not have the statistical power to be relied upon.

However, as q increases, so does the probability that the segment of travel defined by q itself includes other changes of direction. For instance, an animal might wander in a circuitous way for some time, and then begin to travel in a highly directed way, perhaps towards some distant goal. In such a case, higher values of q risk missing the genuine change-point, because the set of q vectors will—since they include circuitous wandering—introduce spurious variance. Indeed, the problem of including spurious variance in the set of q vectors will always arise if q becomes sufficiently high, even if all travel is in wholly linear sectors between change-points. Thus, the optimum value of q is never 'as many as possible': a point will always be reached at which the effectiveness of the CPT will decline. This second, competing trend means that the optimum for any particular study should be estimated empirically with pilot data.

In the case of the Blouberg baboons, we found that the number of change-points detected rose steadily as q increased, up to 6 with $\alpha = 0.01$, but declined thereafter. For Budongo chimpanzees, the peak in overall detection occurred instead at $q = 4$, and in this case the very different ranging characteristics of chimpanzees allowed $\alpha = 0.05$ to be used. We consider that these values would be optimal for analyses of the kinds we set out to do, aiming ultimately to understand the decisions made during foraging. However, with different research aims, researchers might choose to use the CPT in different ways. If avoidance of false positives were critical, then a smaller value of α and in consequence a higher value of q might be optimal (in the case of our chimpanzee data, we also investigated $\alpha = 0.01$ and in this case $q = 6$ was most effective in detecting change-points). Conversely, if the cardinal concern were to identify every change-point, then using multiple values of q might be appropriate. This would pick up both subtle change-points that had the good fortune to occur at locations where circuitous wandering did not mask their presence from high-q variants of the CPT, as well as change-points missed even by otherwise optimal

values of q (e.g. $t = 6$ in our illustrative chimpanzee example, shown in Fig. 8). The corollary would be a necessarily higher risk of false positives. However, only with species with very different travel parameters from those investigated here, for instance travel largely in bee-line routes over very long periods would $q = 1$ be appropriate.

4. **Repeatedly run test(s) to detect change-points**. Starting from the final location of a day or several days' travel, we applied the CPT successively from one change-point to the next, and retrospectively investigated whether these change-points were plausible goals of travel (they were). Alternatively, researchers might use the CPT specifically from a single site known to be a travel goal, for example if a reward were placed experimentally. Note that - log P tends to exceed critical levels in advance of the true change-point when values of $q > 1$ are used. We therefore strongly advocate inspecting the whole series of values of - log P to find the *peak value* of several (significant) values, rather than relying only upon the first significant result to detect the change-point.

Any analysis of a large body of data, especially as in this case one that inevitably involves multiple testing, runs the risk of false positive errors, in which rogue fluctuations are mistaken for change-points. The reality of this risk could clearly be seen in our analysis of synthetic data with higher levels of superimposed noise, when no test variant succeeded in detecting all genuine change-points without also producing some false positives. This problem, however, is no different from that encountered in any data analysis. Wherever there is random variation there will be some unavoidable subjectivity in inference. This is a key fact about all statistical methods, one that causes many people to feel uncomfortable. In the simplest problems there is subjectivity in choosing the significance level, α. In more complicated problems, subjectivity is found also in other quantities specified by the user: the number of components to use in a PCA, the number of correlations to consider in a canonical correlation analysis, the smoothing parameter when fitting a spline for regression—and in the CPT the choice of q. Researchers must always decide upon placement of statistical criteria in the inevitably messy world of real

data. It is just not possible to produce a completely objective sensible procedure for identifying change points; we believe that we have produced a good candidate for a sensible procedure that is 'almost as objective as possible'.

At present, behavioural ecologists have a well tested set of measures—range area, day journey length, foraging rate, diet description in terms of food, energy and nutrient gain, measures of botanical productivity and phenology—that enable meaningful relationships to be detected at the level of groups, populations and species. What is still largely lacking is a good account of how animal cognition affects the strategies available, that is, how individual animals choose their routes (Janson and Byrne 2007). Ultimately, both macro- and micro-level accounts need to be developed and shown to be in accord with each other (just as, in physics, classical and statistical thermodynamics together fully describe heat transfer).

Adding the change-point test to the tool kit of methods applied to the study of animal spatial behaviour has the potential, we believe, to improve analysis of individual decision-making. With the CPT, the points can be identified at which individual animals first begin to travel in the directions that lead them to reach valuable resources, such as feeding sites, water or safe refuges. Additionally, points where direction changes may reflect immediate responses to detection of other individuals, for instance by hearing vocalizations. In both cases these points will often correspond to the outcomes of decision-making processes, individual or group; the exceptions, where the change-points reflect merely the lie of the land, can be set aside on the basis of subsequent examination of the topography. Of course, more is needed before the mental mechanisms of the individuals can be inferred. A change-point before a long period of linear travel ending in stopping to feed is consistent with both (1) a decision to travel with least effort towards an anticipated, remembered resource, and (2) a decision to travel at hazard in a random straight line until food is finally blundered upon. But objectively identifying those points at which travel direction truly changes is the essential first step in understanding how spatial cognition is used in natural environments, and ultimately

whether environmental challenges to spatial abilities have led to evolution of enhanced brain systems for spatial cognition.

Acknowledgements

LAB was supported by a studentship from the Biotechnology and Biological Sciences Research Council (01/A1/S/07457). RN was supported by grants from the following institutions: Zürcher Hochschulverein (FAN), Schweizerische Akademie für Naturwissenschaften, Steo-Stiftung, Goethe-Stiftung, Stiftung Thyll-Dürr, Familien Vontobel-Stiftung, Stiftung Annemarie Schindler, Switzerland, and Russell Trust, Scotland. For permission for LAB to work in Uganda, we thank the Uganda National Council for Science and Technology, the President's Office, the Uganda Wildlife Authority and the Uganda Forest Authority. For help given to LAB in the field, we thank all the staff of the Budongo Forest Project, especially Kakura James, Fred Babweteera, Sean O'Hara, Catherine O'Hara and Vernon Reynolds. For help with preparing the figures, we thank Peter Lindsay. And we thank four anonymous reviewers for their constructive and useful comments, which resulted in substantial improvement to our original version.

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Figure Captions

Figure 1. A 'change-point'. (P.36.) In this hypothetical route, a subject has changed direction in order to reach a resource.

Figure 2. Use of distances in the CPT. (P.37.) A route is viewed as a series of vectors $v_1, v_2, ..., v_n$. The possibility of a change-point between v_2 and v_3 is examined by comparing the distances R_k and R_q with the length of the resultant R_{k+q} (see text).

Figure 3. 'Artificial' routes for evaluation of CPT. (P.38.) In each case, change-point tests were applied from $t = 0$, located at the right border of the panels a – f.

Figure 4. Baboon routes. (P.39.) Top left and bottom right panels show typical dry season routes, top right and bottom left panels show wet season routes. All routes started and ended at the sleeping site ($t = 0$). This was also the location where the first iteration of the CPT started; arrows indicate the direction of testing. Stars indicate significant directional changes at $q = 6$ and $P < 0.01$ (see text for explanations). Grey bars indicate distance of 500 m.

Figure 5. Using the CPT to detect baboon change-points. (P.40-41.) Illustrative example of the application of the CPT applied to the baboon dry season route, shown in the top left panel of Fig. 4 (where arrow indicates test direction). Iterations started at $k = t = 0$, the baboons' sleeping site. We used ten variants with $q = 1, 2, ..., 10$. The x-axis of each panel shows the locations (k) at which the test statistic was computed; the y-axis shows probability P, using a logarithmic scale to aid visual inspection, and dots connected with a solid line show P-values of the CPT at $k = 1, ..., t + 1$. Critical values of the CPT are shown as straight horizontal lines, for $\alpha = 0.1$ (bottom), 0.05 (middle) and 0.01 (top).

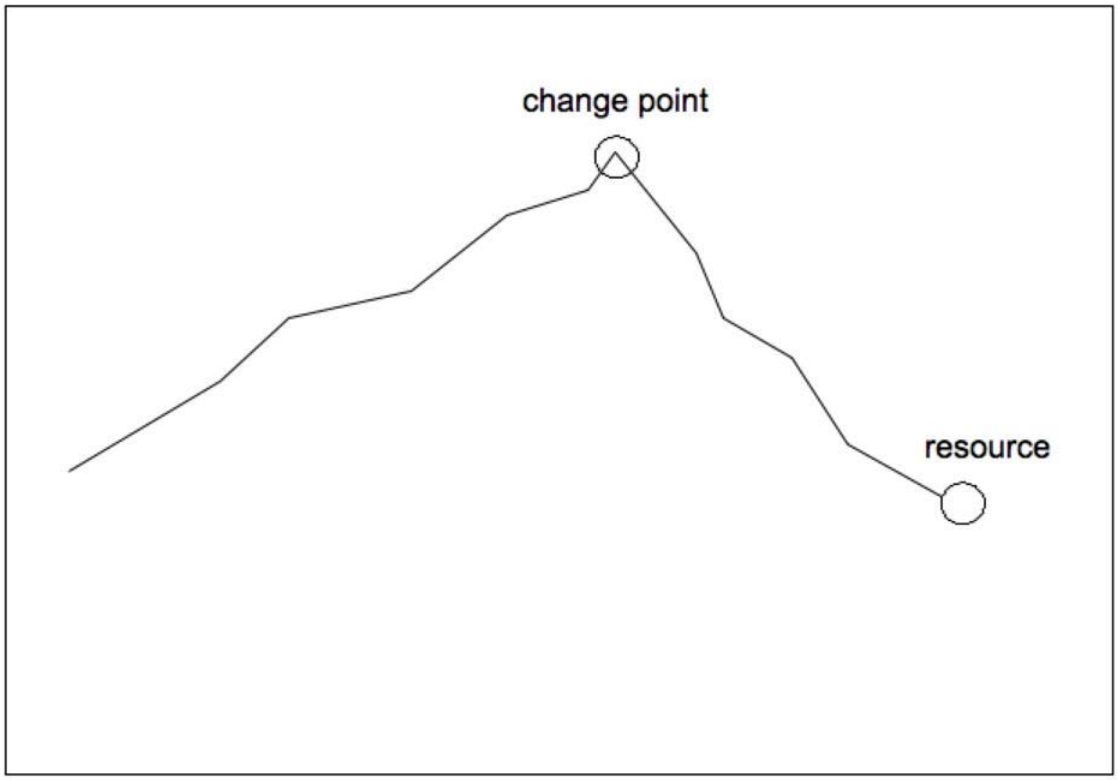
Figure 6. Change-points for baboons at different values of q. (P.42.) The numbers of change-points at different values of q, and at $P < 0.01$, were counted in each of the four baboon routes. The heavy line shows the cumulative numbers of

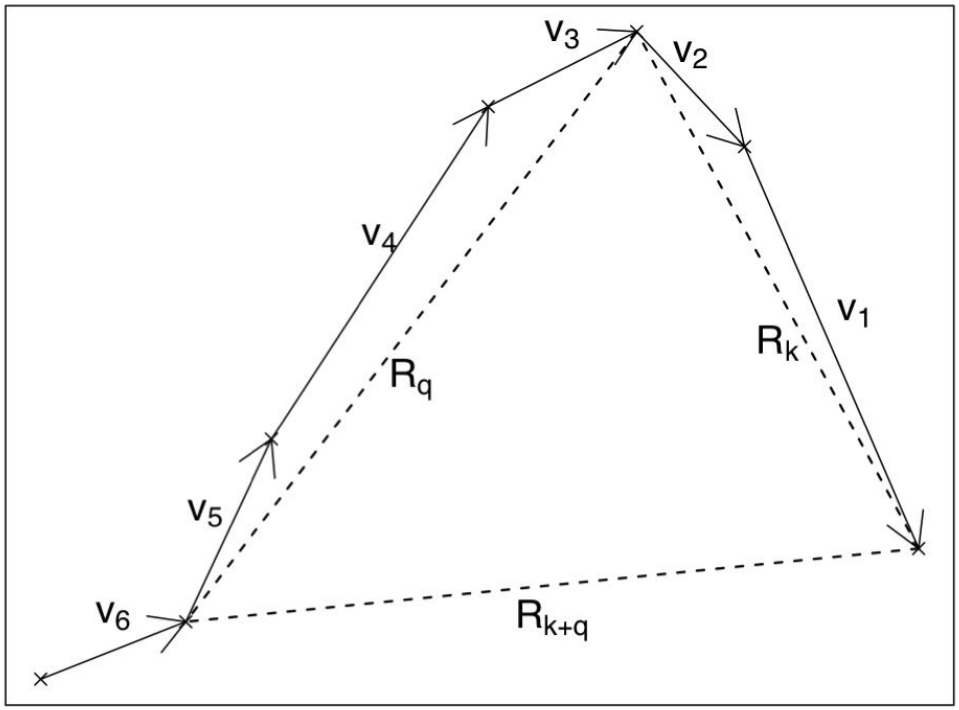
CPs found in the four routes, indicating that the test is most sensitive to directional changes when $q = 6$.

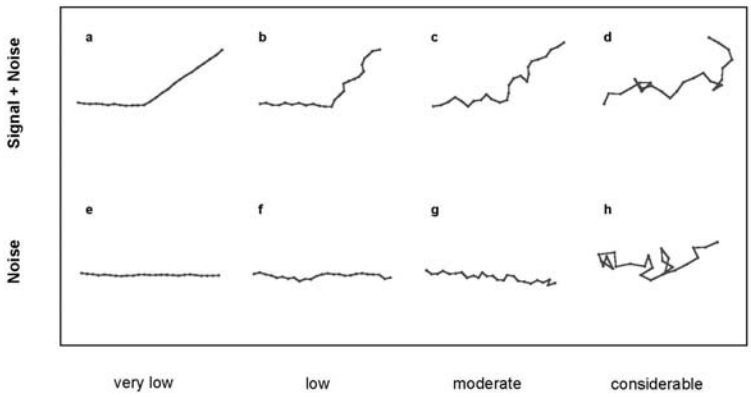
Figure 7. Chimpanzee routes. (P.43.) Panels show routes of four adult male chimpanzees collected over two days. The routes started at the location marked x, and ended at the location marked $t = 0$, from which the first iteration of the CPT was applied. Stars indicate significant directional changes at $q = 4$ and $\alpha = 0.05$.

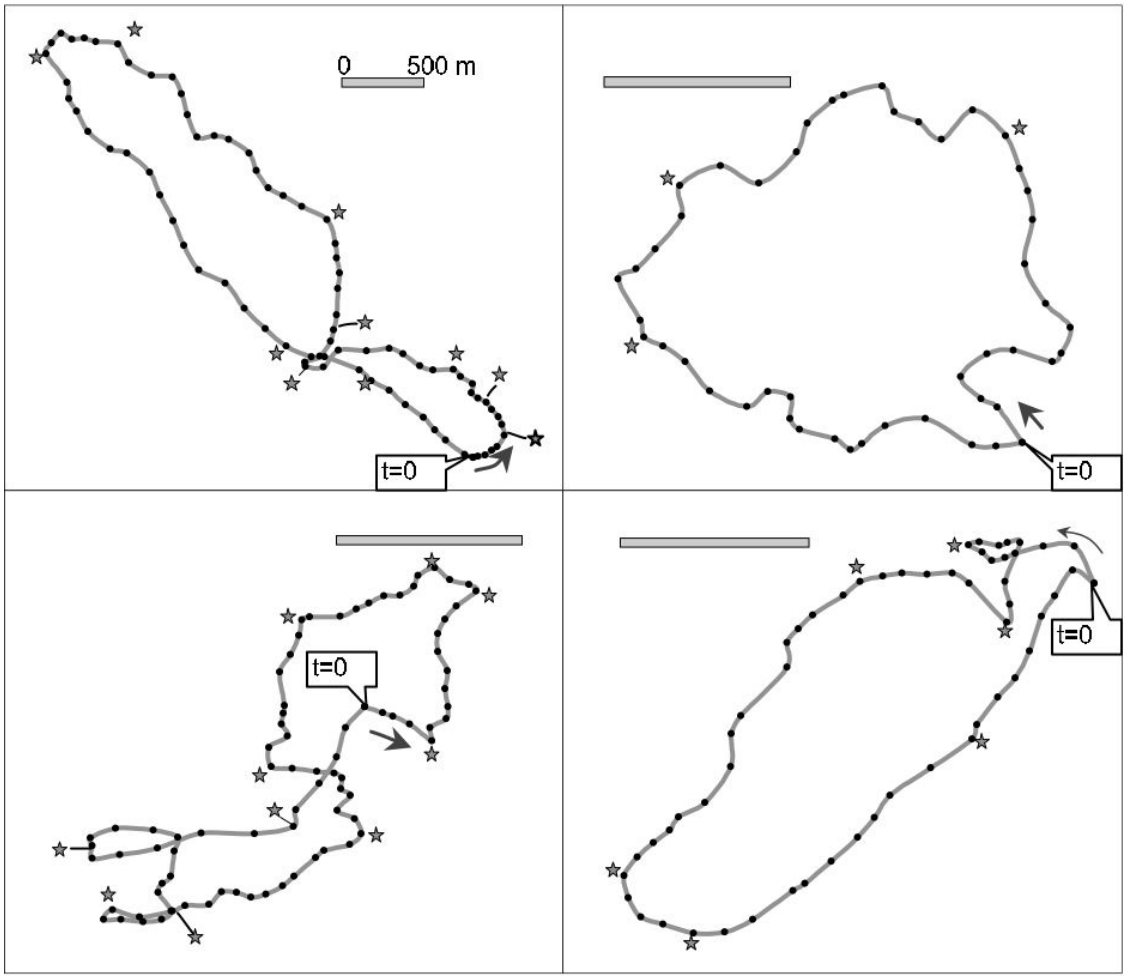
Figure 8. Using the CPT to detect chimpanzee change-points. (P.44.) Illustrative example of the application of the CPT applied to one chimpanzee route, that shown in the top left panel of Fig. 7. Iterations started at $k = t = 0$, the final location recorded in the two-day sample. We used six variants of the test with $q = 1,2,...,6$. The x-axis of each panel shows the locations (k) at which the test statistic was computed; the y-axis shows probability P, using a logarithmic scale to aid visual inspection, and dots connected with a solid line show P-values of the CPT at $k = 1,...,t+1$. Critical values of the CPT are shown as straight horizontal lines, for $\alpha = 0.1$ (bottom), 0.05 (middle) and 0.01 (top).

Figure 9. Change-points for chimpanzees at different values of q. (P.45.) The numbers of change-points detected at $P < 0.05$, with different values of q, were counted in each of the four chimpanzee routes. The heavy line shows the cumulative numbers of change-points found in the four routes, indicating that the test is most sensitive to directional changes when $q = 4$.


change point
resource


v3
v2
v4
v1
Rk
Rq
v5
v6
Rk+q


Signal + Noise
Noise
a
b
c
d
e
f
g
h
very low
low
moderate
considerable


0 500 m
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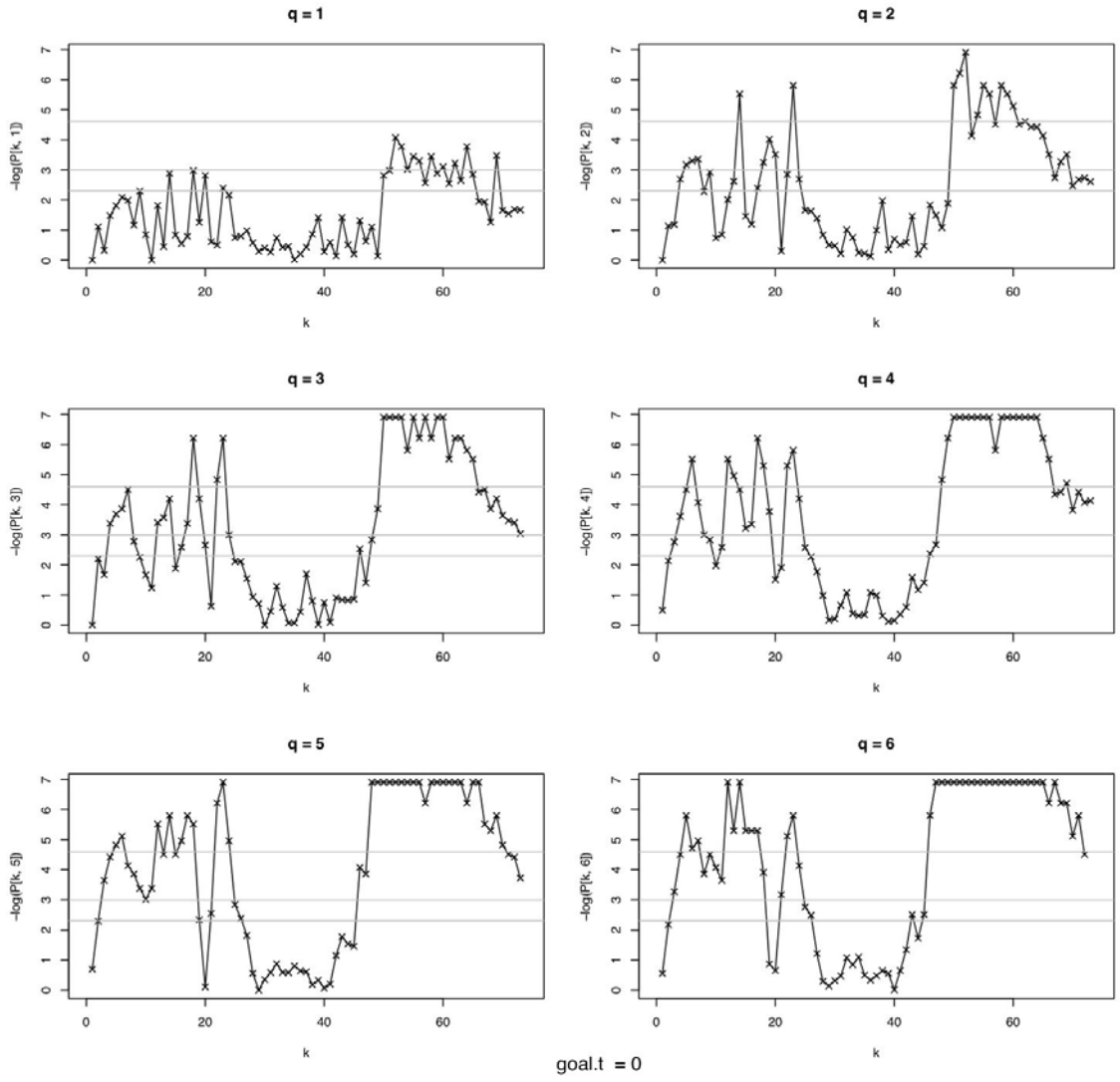
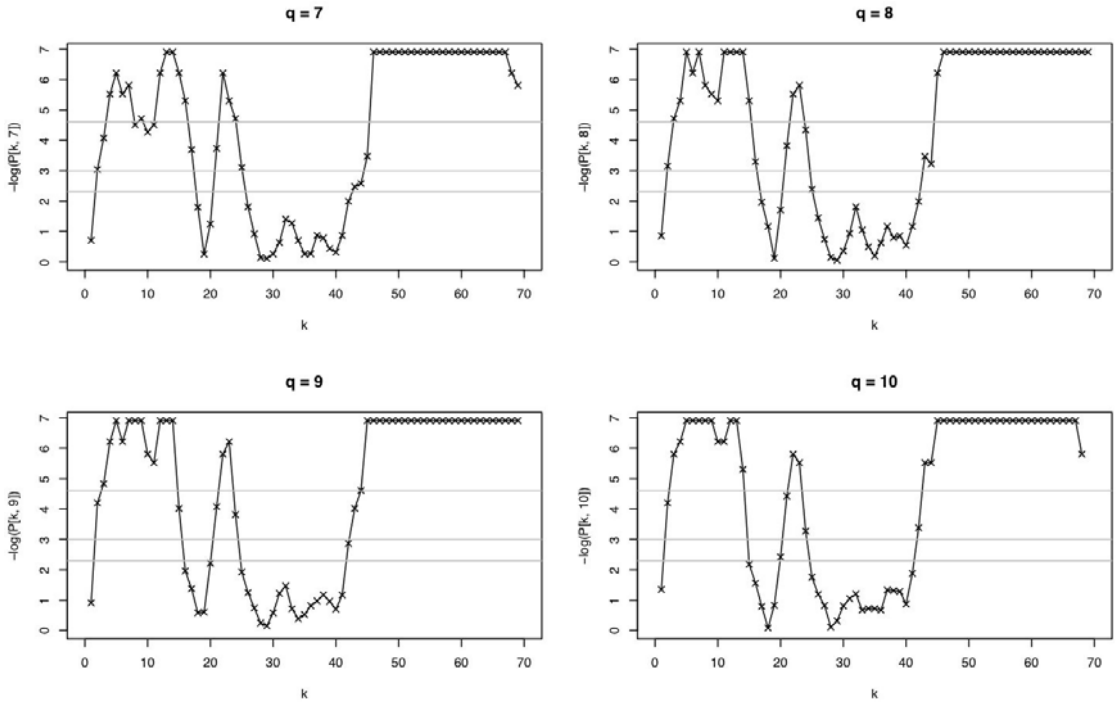
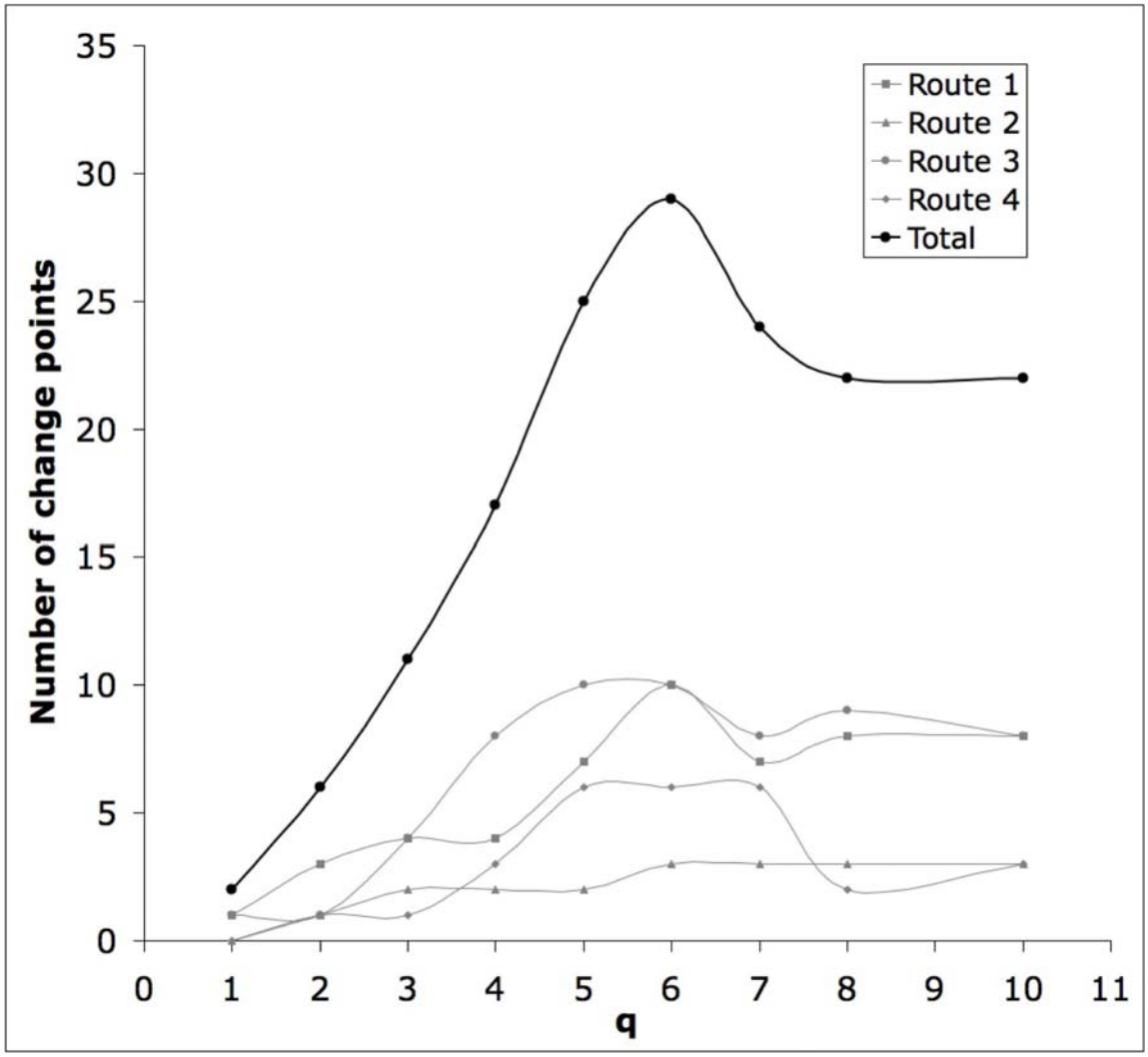
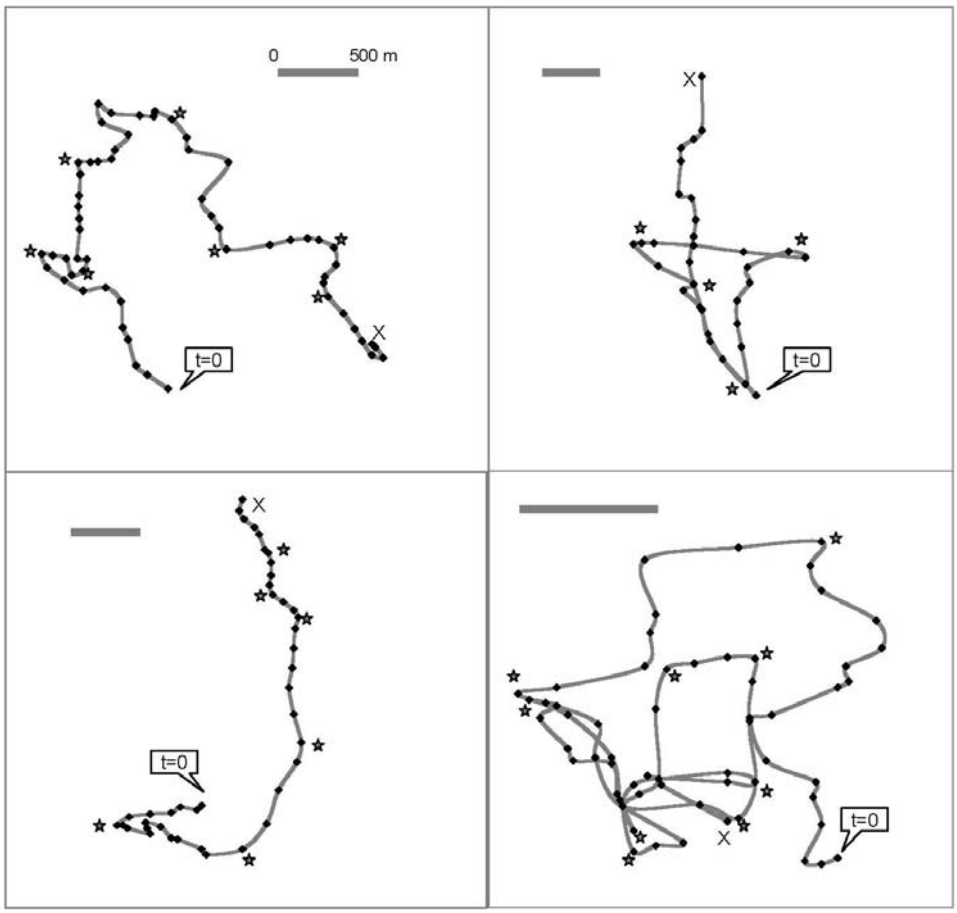
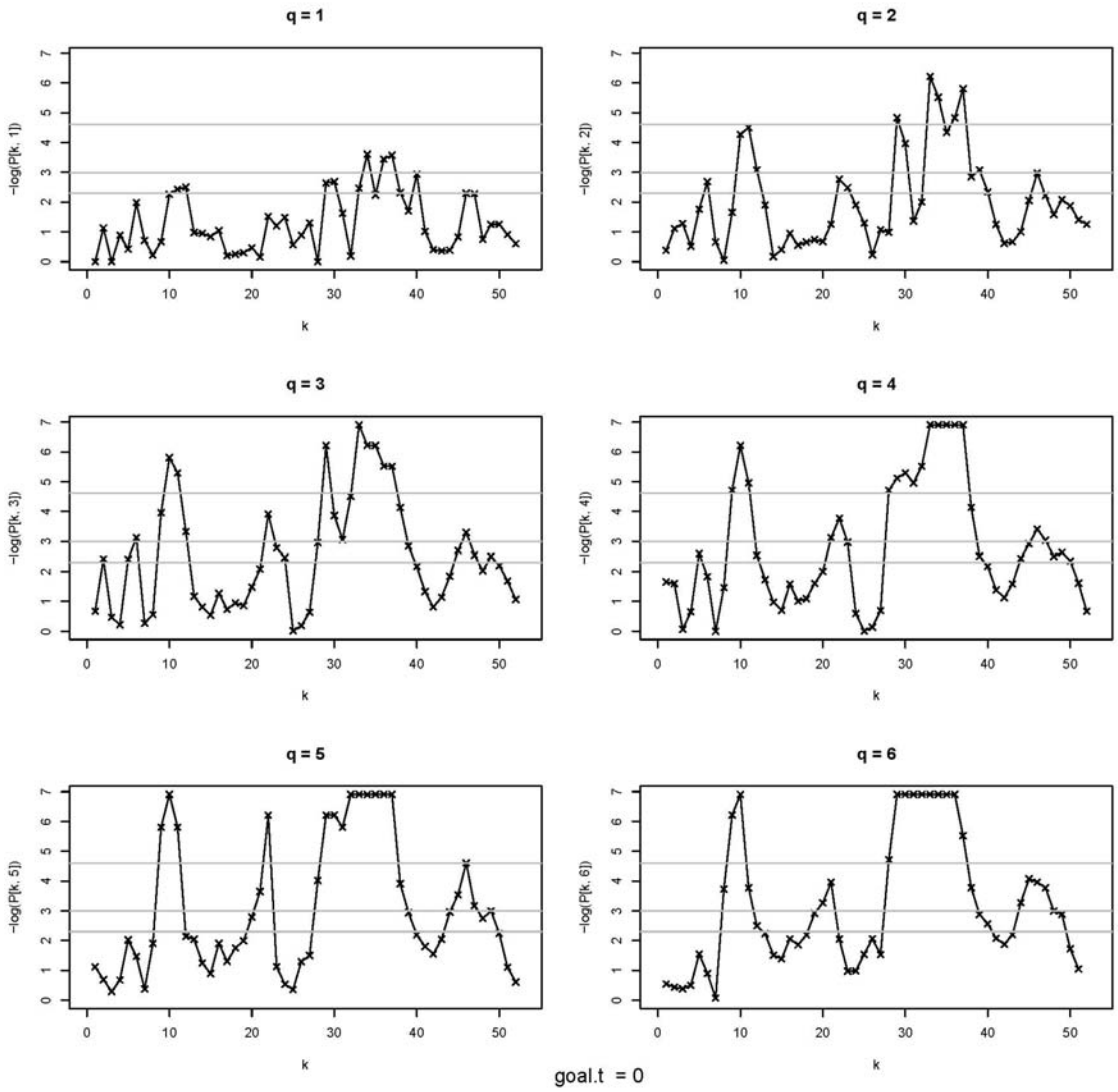
t=0
t=0
t=0

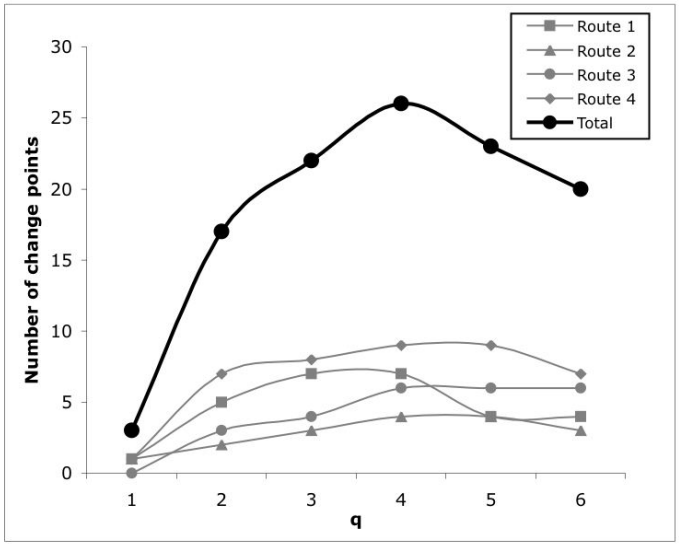

q = 1
q = 2
q = 3
q = 4
q = 5
q = 6
−log(P[k, 1])
−log(P[k, 2])
−log(P[k, 3])
−log(P[k, 4])
−log(P[k, 5])
−log(P[k, 6])
k
goal.t = 0


q = 7
q = 8
q = 9
q = 10
−log(P[k, 7])
−log(P[k, 8])
−log(P[k, 9])
−log(P[k, 10])
k
0
10
20
30
40
50
60
70
1
2
3
4
5
6
7


Route 1
Route 2
Route 3
Route 4
Total
Number of change points
q
0
5
10
15
20
25
30
35
0
1
2
3
4
5
6
7
8
9
10
11


0
500 m
t=0
X
t=0
X
t=0
t=0
X


q = 1
q = 2
q = 3
q = 4
q = 5
q = 6
−log(P[k, 1])
−log(P[k, 2])
−log(P[k, 3])
−log(P[k, 4])
−log(P[k, 5])
−log(P[k, 6])
k
goal.t = 0


Route 1
Route 2
Route 3
Route 4
Total
Number of change points
30
25
20
15
10
5
0
1
2
3
4
5
6
q